# Gastropod Feeding Tracks as a Source of Data in Analysis of the Functional Morphology of Radulae

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*Abstract.* Feeding tracks produced by the radulae of gastropods are potentially rich sources of data that (1) can help explain behavior and behavioral variation, (2) provide dietary evidence of the size, quantity, and specific nature of material that is removed and ingested, and (3) provide detailed evidence of the ways that natural biological materials fail when grazed.

Analysis of feeding tracks of the intertidal trochid *Tegula funebralis* (A. Adams, 1854) on artificial substrates provides standard or idealized sets of impressions of feeding strokes for comparison with sets of impressions of actual interactions of teeth with materials in the normal diet of the species. *Tegula funebralis* feeds in different ways on different substrates by varying the pressure applied to the radula, with results that vary from deep incisions to light brush marks. Different teeth contact the substrate during different feeding behaviors, and various forms of asymmetry are common features of feeding tracks. Feeding tracks can be characterized morphologically on three levels: (1) description of the static pattern of the track, (2) correlation of the incisions with the teeth that produced them, and (3) dynamic specification of the order in which individual incisions and groups of incisions are produced relative to the morphology and movements of the apparatus. The most accurate level of documentation requires frame-by-frame analysis of filmed feeding sequences of living animals.

## INTRODUCTION

MOVEMENT AND FUNCTION of radular teeth and the nature of their interactions with food items and substrates are among the least well understood aspects of gastropod feeding. Function cannot be inferred from tooth form alone (HICKMAN, 1980) or even from correlations of tooth form and gut contents (HICKMAN, 1981b). In an earlier paper (MORRIS & HICKMAN, 1981) we emphasized the importance of configuration changes in the cylindrical radula of *Tegula funebralis* (A. Adams, 1854) in producing a complex sequence of tooth movements during protraction and retraction. The purpose of this paper is to document the results of the basic feeding stroke of this rhipidoglossan trochid gastropod on both artificial and natural substrates and to show how the stroke can be modified behaviorally to produce different results. Demonstration that *T. funebralis* can use its radula to feed in different ways on different substrates argues for caution in interpreting correlations between tooth morphology and diet. On the other hand, a wealth of detailed information is available in radula-marred substrates and prey items, and we hope to stimulate interest in the morphology of feeding tracks as a source of functional inference.

Correlations between tooth form and diet are most common in specialized feeders. Some of the best documentations in marine gastropods are for *Conus* (NYBAKKEN, 1970)

and "grazing" carnivorous nudibranchs (McDONALD & NYBAKKEN, 1978; NYBAKKEN & McDONALD, 1981). However, the specific nature of radular damage to prey or interaction with the prey is not understood.

Characterizations of radula-damaged substrates are rare in the literature. Attention to substrate morphology has focused primarily on specialized systems, such as the morphology of boreholes produced by active predatory marine prosobranchs (CARRIKER, 1961, 1977; RADWIN & WELLS, 1968), or characteristic damage to foraminiferal tests produced by *Olivella* (HICKMAN & LIPPS, 1983). Surfaces of grazed substrates are the least well known but potentially rich sources of functional data. The potential is particularly well illustrated by STENECK, who has figured grazing incisions in crustose coralline algae at the level of cellular resolution (1982, fig. 5c; 1983, fig. 2) and estimated the number of epithelial cells consumed per bite by an acmaeid limpet (1982:512). However, as in the accounts of a correlative morphological nature, details of function are not understood relative to the incisions.

From a sedimentological viewpoint, there has been some interest in bioerosive damage to calcium carbonate substrates as a by-product of molluscan grazing. Some chitons and acmaeid limpets excavate shells to feed on boring algae (GOLUBIC *et al.,* 1975; FARROW & CLOKIE (1979). The importance of this process is emphasized by FARROW & CLOKIE (1979) who conclude that molluscan feeding is a major factor in recycling of carbonate from shells and in producing carbonate mud in a shallow seaway in Scotland.

From the perspective of geologic time, molluscan feeding traces on carbonate substrates have been reported as far back as the Upper Jurassic (BOEKSCHOTEN, 1967; VOIGT, 1977). At least some of these fossil grazing traces seem to be associated with algal-bored substrates (TAYLOR, 1981; AKPAN *et al.,* 1982). Because many of the fossil traces are closely similar in morphology to modern traces associated with chitons and acmaeid limpets, functional and behavioral interpretations should be possible once the modern traces have been analyzed correctly in functional terms.

Feeding track morphology has been studied most extensively by European biologists on aquarium walls or algal-coated plates (*Algen-platten*) (HUBENDICK, 1957; ANKEL, 1938; EIGENBRODT, 1941) and on glass surfaces coated with wax (*Fettplaten*) (MÄRKEL, 1957, 1966). It is these studies that inspired us to elaborate and extend the approach to a comparison of artificial surfaces with natural surfaces and items in the diet of *Tegula funebralis.*

## MATERIALS AND METHODS

To obtain a baseline description of the *idealized* feeding track (*i.e.,* tooth impressions produced by a single feeding stroke), it is necessary to have a flat, smooth, fine-grained surface that will retain three-dimensional impressions. It also must be a material to which snails are willing to

apply the radula. Experimentation with a variety of waxes and preparation techniques led to a procedure using beeswax (MORRIS, 1980).

To produce a smooth, shiny surface, melted (60°C) paper-filtered unpurified beeswax (Bee, Inc.) was poured 4 mm thick on cellophane stretched over 2.5-cm high aluminum rings supported by upside-down petri dish tops. After cooling to room temperature, individual beeswax disks were placed in a freezer for 1 h to harden. Rapid peeling of the cellophane membrane from the frozen wax produced a shiny surface.

*Tegula funebralis* would not graze on new disks, but feeding tracks were readily obtained on disks that had been "cured" for one week in aerated natural seawater at 7°C. Individual snails were restricted to separate cured disks in finger bowls covered with porous polyethylene covers, so that feeding tracks could be correlated with specific radulae.

After washing grazed disks in distilled water, a great deal of information can be obtained by examining feeding tracks on dry disk surfaces with a dissecting microscope and low-angle reflected light. The illustrations in this paper were obtained with scanning electron microscopy from portions of disks removed with a hot scalpel, mounted on SEM stubs, and coated with gold palladium. Scanning electron microscopy permits resolution of individual tooth excavations at higher magnifications than are obtainable with a light microscope.

To obtain comparable observations of the effect of the feeding stroke on irregular surfaces and natural textures of the food items in the diet of *Tegula funebralis*, individuals were allowed to graze in covered finger bowls on three algal species. *Laminaria dentigera, Iridaea splendens,* and the sporophytic rock-encrusting form of *Gigartina* sp. (formerly referred to *Petrocelis* sp.) were chosen to cover a range of variation in surface texture and topography. *Tegula funebralis* has been observed feeding (making the behavioral motions that indicate protraction and retraction of the radula) on all three species in the field, as well as on a variety of other algae (authors' personal observations); and BEST (1964) concluded from experimental studies that, although *T. funebralis* prefers fleshy macroalgae, it feeds on a variety of encrusting species as well.

Sections of algae with feeding tracks were cut out and fixed in 2.5% glutaraldehyde, postfixed in 1% osmium tetroxide, dehydrated through an ethanol series from 50% to 100%, and critical point dried. Dried specimens were coated with gold palladium and viewed over the same range of magnifications as the traces on the beeswax surfaces.

## RESULTS

### Feeding Tracks on Beeswax

**Idealized tracks:** Typical tracks of *Tegula funebralis* on beeswax surfaces are illustrated in Figures 1–8. Each track is the result of a single feeding stroke or cycle of radular

protraction and retraction. During the feeding stroke the radula behaves as a flat band anteriorly and a slit cylinder posteriorly, with a movable semicircular crease at the region of transition that is controlled by the underlying odontophore. The configuration of the radula at maximum protraction is illustrated in Figure 9, and the cylindrical mode of function is outlined by MORRIS & HICKMAN (1981).

Each trace has two parts and is roughly bilaterally symmetrical. In a typical trace the two opposing incised regions are produced exclusively by marginal teeth and are separated by an untouched central region (Figures 1, 2). Although the rachidian and lateral teeth are the largest teeth in the radula, they are recessed between the tips of the odontophore and do not normally contact flat substrates during the feeding stroke.

The most prominent portions of the trace are the curved incisions of the individual innermost marginal teeth. Three or four rows of teeth are involved in the production of each trace. The sequence of movements is not intuitively obvious from the morphology of the apparatus, and the description of trace production is derived from frame-by-frame analysis of feeding strokes filmed through a microscope on plexiglass surfaces.

Traces in Figures 1–7 are all oriented with anterior at the top. Note that anterior and posterior correspond to the positions of the anterior (dorsal) and posterior (ventral) lips of the mouth as it is applied to the substratum. Thus the anterior end of each trace represents the leading edge of the direction of locomotion of the snail. In this usage, anterior and posterior on the trace do not correspond to anterior and posterior on the radula itself. Because the radula operates as a slit cylinder (MORRIS & HICKMAN, 1981), anterior and posterior rows of teeth are arranged concentrically, so that posterior is in the center and anterior is at the periphery (Figure 9). As a consequence of this configuration, the anterior end of each trace is made by the posterior rows of teeth and the posterior end of each trace by the anterior tooth rows.

The dominant mark in each trace is the single long and deep incision of the innermost marginal (Figures 1–4). Adjacent and anterior to the dominant incision is a series of successively shorter and shallower traces of the remaining five or six inner marginal teeth of the same row (Figures 1–4). This unit is repeated three to five times by the rows of inner marginal teeth that contact the substrate during the feeding stroke.

Figure 10a shows the relative positions and configuration of three marginal tooth rows at the beginning of the feeding stroke and the travel paths of the inner marginal teeth. From this diagram it should be clear why the posteriormost row strikes the substrate first to form the anteriormost unit of the trace; why the sequence of substrate contact within a row is from outer to inner marginals; and, finally, why the innermost dominant incision is the posteriormost incision in each unit on the substrate.

The path followed by a single row of teeth during the feeding stroke is illustrated diagrammatically in Figure 10b. Only those portions of the row that pass directly over the odontophore and make substrate contact are illustrated. The heavy lines are successive tracings of the position of the row in sampled frames from 0 to 40 in one filmed feeding stroke. Zero represents maximum protraction and 40 represents the point at which the row leaves the substrate. Another way to view the same sequence is to follow the paths of individual teeth or groups of teeth. Figure 10c diagrams the paths of different major blocks of marginal teeth. Movement is toward the central axis of the diagram. On such a diagram, we can trace the path of any individual tooth from the point of initial contact to the point of lifting from the substrate. These two diagrams together further help explain why the sequence of contact of teeth in any given row is from outer to inner marginals and why the trace records the sequence in an anterior to posterior direction.

One final set of principles will be helpful in understanding the production of the trace. First, it is the inner marginals that move most directly over the tips of the two horns of the odontophore as substrate contact is made. Second, rates of travel vary for different sections of a single row, and the inner marginals act quickly, in a rapid "snapping" of the teeth as they flip over the cartilage at the inner edge of the *knickstelle* or semicircular crease. Third, facilitation of inner marginal "snapping" is furthered by the movement of the crease itself as the odontophore is drawn posteriorly during the feeding stroke. Fourth, the pointed cusps are rotating as they gouge the substrate to produce U-shaped incisions. Figure 8 is a low-angle micrograph showing the profiles and relative depths of incisions.

**Variations:** In contrast to the typical feeding track described above, some feeding tracks are dominated by fine brush marks of the mid and outer marginal teeth. Unlike the inner marginals, mid and outer marginal cusps do not make separate incisions. The upper surfaces of the cusps act in close concert as they are pressed against a flat substrate and drawn over it. The feeding stroke can be varied so that only brush marks are produced. Figure 5 shows a trace with both incisions and brush marks, while Figures 6 and 7 show traces that are dominated by mid and outer marginal brush marks.

A number of other variations appear in feeding tracks on the beeswax substrates. The number of rows that contact the substrate is variable (*i.e.,* the number of times that the basic unit is repeated from anterior to posterior. Furthermore, the number can vary from one side of the trace to the other, disrupting the bilateral symmetry (Figure 2). This kind of variation occurs because the right and left tips of the odontophore act independently and do not necessarily exert the same pressure on the right and left sides of the radula. Asymmetric traces can be produced in other ways, some of which are related to underlying patterns of asymmetry in the morphology itself (HICKMAN, 1981a,
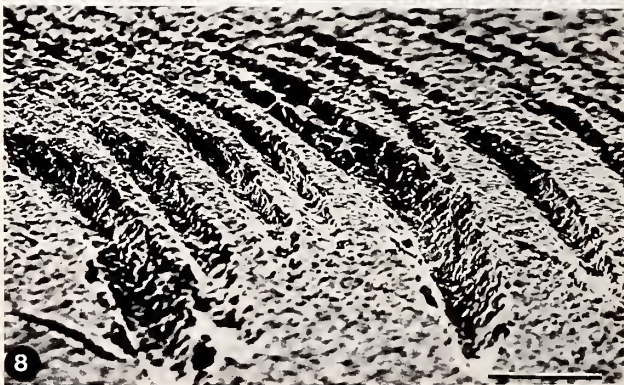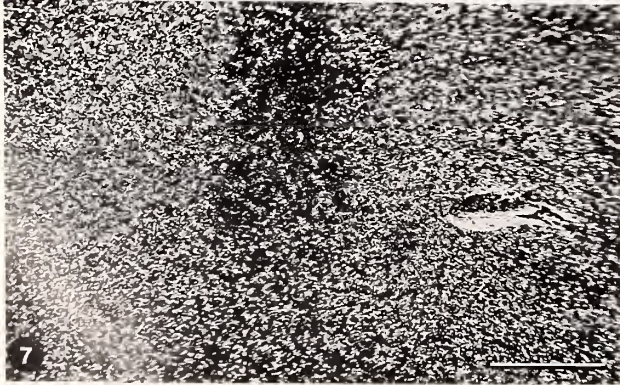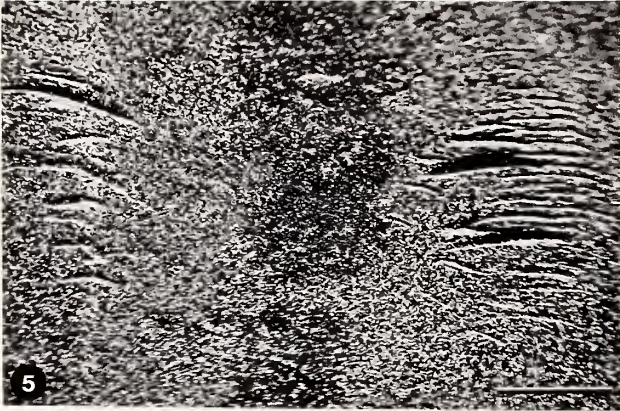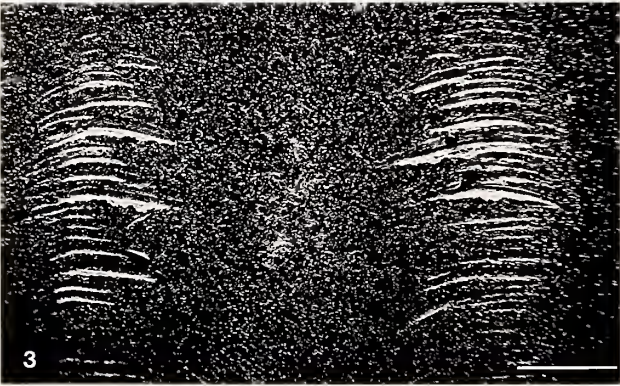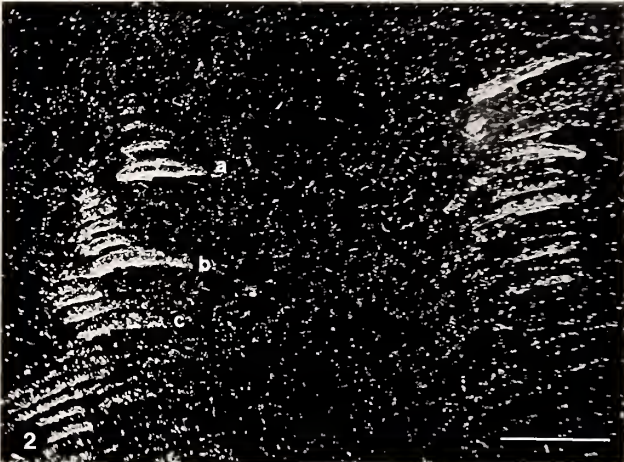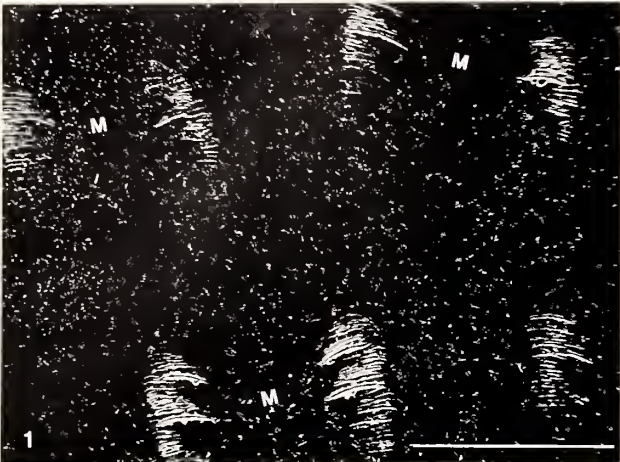
1984), although behavioral asymmetries are more conspicuous in feeding tracks. For example, if the tips of the odontophore do not move synchronously (*i.e.,* if one is applied to the substrate in advance of the other) a trace may be produced in which one half will lie anterior to, or offset from, the other half (Figures 2, 6). Finally, if the tips of the odontophore do not move straight back (*i.e.,* parallel to the plane of symmetry of the idealized trace, the radula, and the head/foot), a curved trace will be produced. Figure 6 is a trace that was produced by odontophore tips both moving in parallel arcs. These are the most common forms of variation, although others occur, and they can be interpreted from what we know about tooth morphology, our knowledge of radular function, and by comparison with the idealized trace.

## Feeding Tracks on Natural Substrates

In nature, *Tegula funebralis* does not graze on beeswax or plexiglass, nor is it likely to encounter other surfaces that are perfectly flat and homogeneous. Examination of feeding tracks on algal surfaces confirms that the radula is used differently on different food items in the natural diet of the snails (Figures 11–14).

On the relatively flat blades of the brown alga *Laminaria dentigera* (Figures 11, 12) animals may leave paired sets of inner marginal incisions similar to those of the idealized feeding tracks on beeswax. As on the beeswax, the depth of incision is variable, and the tracks are frequently asymmetric. This type of incision was observed to release copious cell contents, which are preserved dried in Figure 11. In this form of feeding, no algal tissue is removed by the radula.

It would be tempting to conclude that *Tegula funebralis* feeds on cell sap of *Laminaria*. However, animals also produce much deeper paired excavations on algal blades. Figure 13 shows an excavated feeding track from which
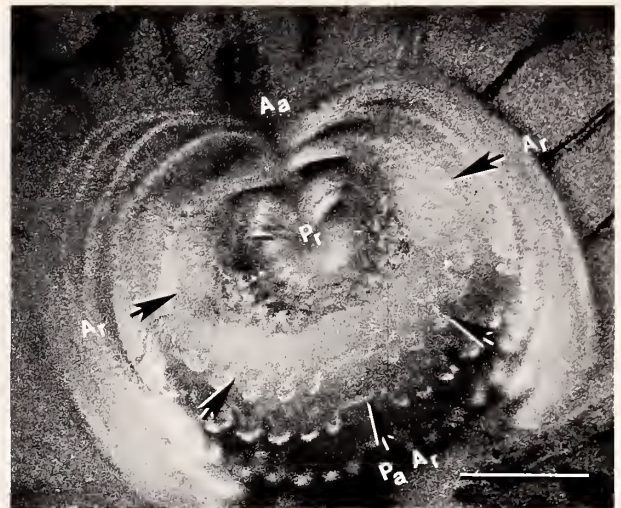


Figure 9

Optical micrograph of living *Tegula funebralis* with radula protracted, from 35-mm negative. Note subcylindrical configuration with concentrically arrayed tooth rows. Anterior rows on the radula ($A_r$) are on the outside, while posterior rows ($P_r$) are in the center. $A_a$ denotes anterior lip of the animal; $A_p$ denotes posterior. Arrows show direction of row movement during retraction. Bar = 0.5 mm.

a significant volume of algal tissue has been removed. It does not seem possible that a single feeding stroke could have produced all this damage to the laminarian blade, and this may represent a series of feeding strokes "in place."

On the irregular blade surfaces of the red alga *Iridaea splendens,* feeding traces indicate yet another mode of feeding. Figure 14 shows a surface that has been brushed free of its attached microbiota with no sign of damage to the underlying blade. This light brushing of the surface by

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## Explanation of Figures 1 to 8

Scanning electron micrographs of feeding tracks of *Tegula funebralis* on cured beeswax surfaces. Figures 1–7 are oriented with anterior ends of traces up. Note that in this orientation the order of trace formation is from top to bottom, with posterior rows striking the surface first.

Figure 1. Low magnification view of three separate traces, each produced by a single feeding stroke; M = the center of each trace. Bar = 1 mm.

Figure 2. Asymmetric feeding track produced by a single feeding stroke in which the left side is farther anterior and more disorganized due to independent behavior of the two tips of the odontophore. a, b, c = incisions of the innermost marginal teeth of three successive rows. Compare with Figure 10a for orientation. Bar = 400 μm.

Figure 3. Single feeding track made by inner marginal teeth. Bar = 400 μm.

Figure 4. Left half of an asymmetric feeding track with relatively deep inner marginal incisions. Note that at least 11 inner marginal teeth in the posteriormost row (anterior or top on the trace) contacted the substrate. Bar = 400 μm.

Figure 5. Feeding track showing both inner marginal incisions and mid and outer marginal brush marks. Bar = 400 μm.

Figure 6. Strongly asymmetric feeding track consisting of mid and outer marginal brush marks. Bar = 400 μm.

Figure 7. Bilaterally symmetric feeding track consisting of light mid and outer marginal brush marks. Bar = 400 μm.

Figure 8. Low-angle side view of left half of feeding track showing incisions of inner marginal teeth. Longest and deepest incisions are those of the innermost marginal; anterior is at right; individual tooth movement was from top to bottom; and sequence of incisions is from right and to left. Bar = 100 μm.
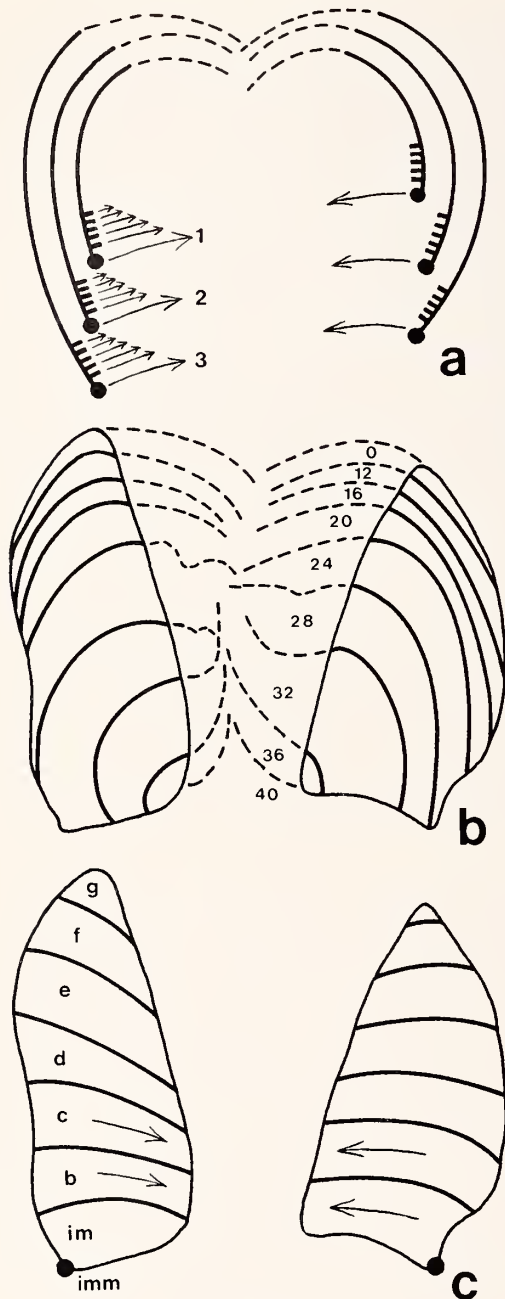
Figure 10

Dynamics of feeding track production, illustrated from analysis of 16-mm slow motion (64 frames/sec) film of *Tegula funebralis* on wall of plexiglass aquarium. a. Position of three rows at beginning of feeding stroke (compare with Figure 9). Arrows show paths of marginal teeth (dominant inner marginal is represented by large dot); Row 1 (posteriormost on radula) passes over odontophore and strikes substrate first, followed by rows 2 and 3 (anterior on radula). Solid lines are portions of rows that make substrate contact. b. Diagram of successive tracings of the position of a single row over 40 frames in one filmed feeding stroke. Solid lines show row in contact with substrate; broken lines show position of retracted portions of rows no longer in

mid and outer marginal teeth is achieved through lessening the pressure applied to the radula by the odontophoral cartilage and is comparable to the type of brush track recorded on beeswax in Figures 6 and 7. This mode of feeding was also observed in snails feeding on the surface of the crustose sporophytic form of *Gigartina* spp. (formerly referred to as *Petrocelis franciscana*).

### DISCUSSION and CONCLUSIONS

Feeding tracks can be "described" on three levels. The morphology of the trace can be characterized most simply as a pattern of marks on the substrate. It also can be characterized by attributing individual marks to individual teeth or groups of teeth (a correlation of one static pattern with another). It can be characterized further at a dynamic level, as a temporal sequence that specifies the order in which individual marks and groups of marks are made relative to the complex ordering of movements of the radula and odontophore.

The first-order pattern can be described without reference to its production. The description, however, need not lack detail: a first-order description at high magnification of the ways that cell walls or the underlying biological materials have failed may contain a great deal of information. The second order of complexity requires knowledge of the morphology (and perhaps composition and structure) of the objects that contact the substrate to produce the trace. And the third order of complexity requires knowledge of how the morphology moves and works.

The methods and results outlined above provide a guide to description and analysis at each of the three levels. They also provide a direct approach to integrated understanding of radular functional morphology incorporating substrate data. It is not clear why so little attention has been paid to substrate data. Perhaps it is the combination of the microscopic scale of most feeding traces, their inconspicuousness, and the difficulty of observing, preserving, and collecting them in the field along with the individual animals that produced them.

To ignore substrate data, however, is analogous to attempting to analyze what a pencil is used for and how it functions by examining the pencil and watching someone manipulating it without ever examining how it is applied to a piece of paper or what appears on the paper. The marks on the paper are, in this instance, a particularly rich source of information about the functional possibilities of a pencil.

The approach that we advocate can be taken much further than we have taken it here. For example it can be

contact. c. Diagram of paths of movement of major blocks of teeth in a single row over the same 40-frame sequence depicted in B. imm = innermost marginal tooth; im = inner marginal tooth block (teeth producing incisions), and b–g = mid to outer marginal blocks.
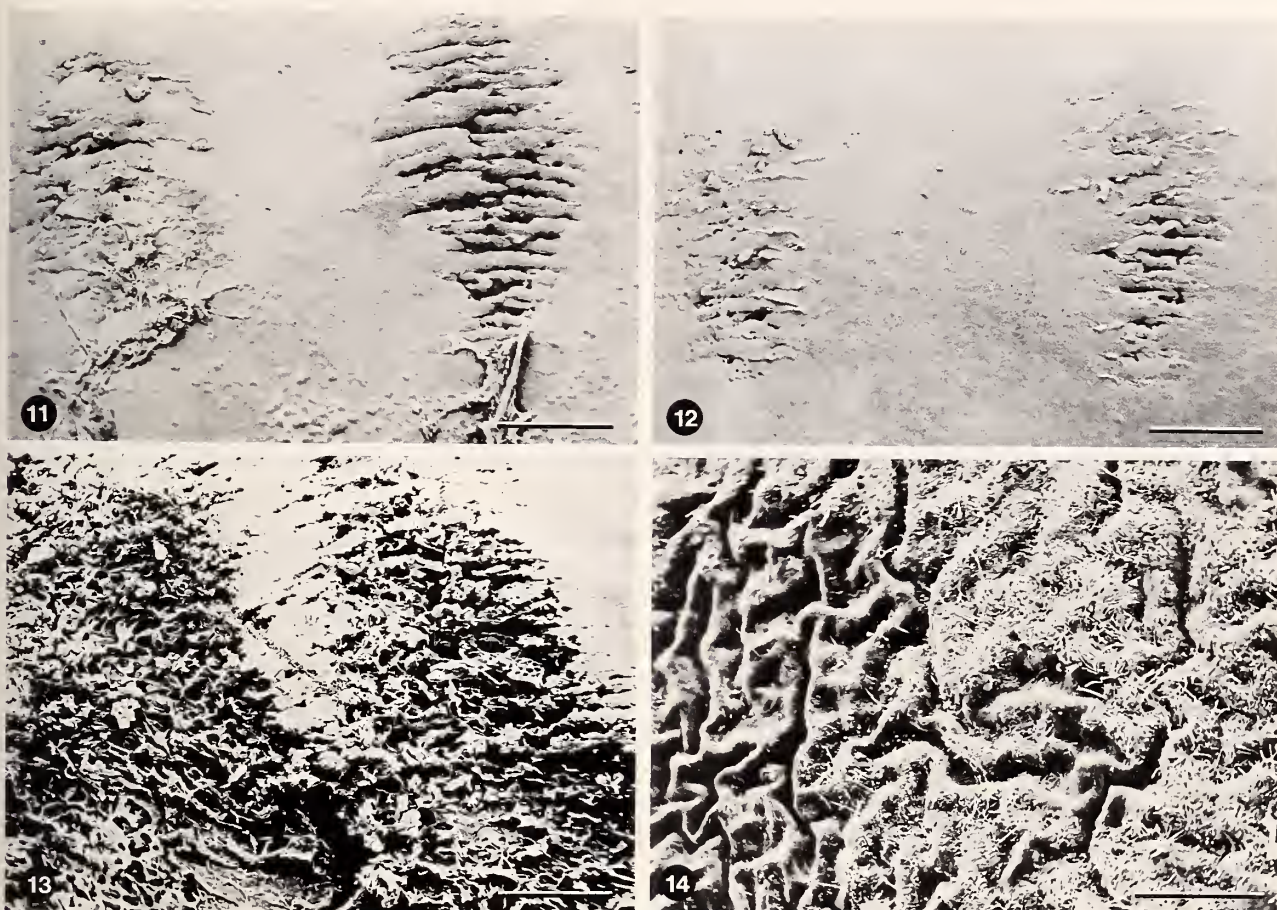
## Explanation of Figures 11 to 14

Scanning electron micrographs of surfaces of macroalgae after grazing by *Tegula funebralis*.

Figure 11. Flat surface of *Laminaria dentigera* with inner marginal incisions and dried cell contents (at posterior end of each half of the feeding track). Bar = 400 μm.

Figure 12. *Laminaria dentigera* with single, lightly incised feeding trace. Bar = 400 μm.

Figure 13. *Laminaria dentigera* with paired deep excavations and algal tissue removed, probably the result of multiple feeding strokes in place. Bar = 400 μm.

Figure 14. Topographically irregular surface of *Iridaea splendens* with ungrazed microbiota on right and surface brushed free of epibionts on left. Bar = 40 μm.

extended to include consideration of the biomechanical properties of radulae and substrates and their interactions. LITTLER & LITTLER (1980) and STENECK & WATLING (1982) have suggested that both algae and algal grazers can be arrayed in "functional groups" related to estimated "toughness" of the alga and estimated "excavating abilities" of the feeding apparatus. Comparative study of radular morphology, methods of application of radulae to substrates, and feeding tracks point to major biomechanical difficulties with these predictions. Toughness may be an important property of *some* algae relative to *some* of the tools that *some* gastropods apply in *some* of their feeding behaviors. For other gastropods, other biomechanical properties of radular teeth and other biomechanical prop-

erties of substrates than toughness may be important. This is suggested by the radular morphology and composition, the method of function, and the substrates upon which some docoglossan limpets feed. Figure 15 illustrates the feeding tracks of *Collisella asmi* (Middendorff, 1847) incised in the calcium carbonate shell of its host, *Tegula funebralis*. The significant properties of the mineral substrate are its brittleness and hardness relative to the brittleness and hardness of the heavily mineralized radular teeth. The significant feature of the manner in which this radula is drawn across the substrate and the linear grooves that result (Figure 15) is the abrasive mode of removal of material (which occurs in the gut in finely divided form). Note that the incisions in Figure 15 are produced parallel
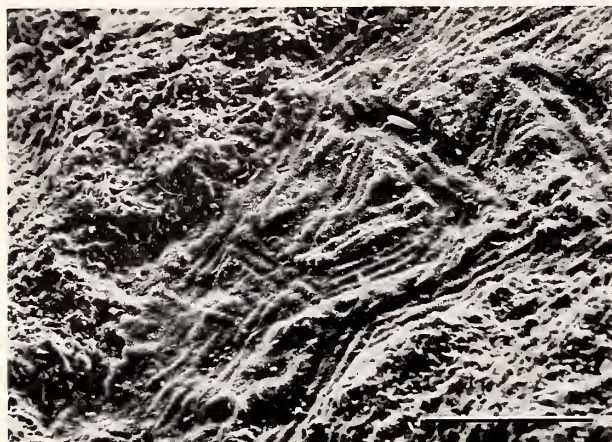
Figure 15

Feeding tracks of *Collisella asmi* incised in the shell of *Tegula funebralis*. Each individual feeding stroke consists of four parallel grooves produced by abrasion from two inner lateral and two outer lateral tooth positions. Bar = 100 µm.

to the longitudinal axis of the radular ribbon, in contrast to the incisions of the radula of *T. funebralis*, which are normal to the axis. Wear patterns of individual docoglossan teeth are related to this abrasive mode of feeding (RUNHAM & THORNTON, 1967; KERTH, 1983) and, contrary to most wear patterns, the teeth maintain a sharp, efficient edge by virtue of use (HICKMAN, 1980).

Aside from applicability to functional morphological analysis and its biomechanical extensions, feeding track data can provide better documentation of gastropod feeding biology. Tabulations of dietary preferences of gastropods (see STENECK & WATLING, 1982, appendix 1 and references therein) are based primarily on observed substrate associations and gut contents. Feeding tracks provide more reliable and visually compelling estimates of what animals have actually taken from the substrate— liquid cell contents, tissue, surface epiphytes, *etc.* First-order observations are adequate for dietary documentation.

A final extension of feeding track analysis is into experimental ecology and tests of feeding theory. Substrates can be used experimentally to document and compare patterns of coverage and coverage efficiency, to produce estimates of materials removed per unit time, and to examine patterns of substrate use and partitioning in both single and multi-species systems.

## ACKNOWLEDGMENTS

## LITERATURE CITED

AKPAN, E. B., G. E. FARROW & N. MORRIS. 1982. Limpet grazing on Cretaceous algal-bored ammonites. Palaeontology 25:361–367.

ANKEL, W. E. 1938. Erwerb und Aufnahme der Nahrung bei den Gastropoden. Verhandl. Deutschen Zool. Gesellsch. Suppl. 11:223–295.

BEST, B. 1964. Feeding activities of *Tegula funebralis*. Veliger 6(suppl.):42–45.

BOEKSCHOTEN, G. J. 1967. Palaeoecology of some Mollusca from the Tielrode Sands (Pliocene, Belgium). Palaeogeogr. Palaeoclimatol. Palaeoecol. 3:311–362.

CARRIKER, M. E. 1961. Comparative functional morphology of boring mechanisms in gastropods. Amer. Zool. 1:263–266.

CARRIKER, M. E. 1977. Ultrastructural evidence that gastropods swallow shell rasped during hole boring. Biol. Bull. 152:325–336.

EIGENBRODT, H. 1941. Untersuchungen über die Funktion der Radula einiger Schnecken. Z. Morphol. Ökol. Tiere 37: 735–791.

FARROW, G. E. & J. CLOKIE. 1979. Molluscan grazing of sublittoral algal-bored shells and the production of carbonate mud in the Firth of Clyde, Scotland. Trans. Roy. Soc. Edinburgh 70:139–148.

GOLUBIC, S., R. D. PERKINS & K. J. LUKAS. 1975. Boring microorganisms and microborings in carbonate substrates. Pp. 229–259. *In:* R. W. Frey (ed.), The study of trace fossils. Springer: Berlin.

HICKMAN, C. S. 1980. Gastropod radulae and the assessment of form in evolutionary paleontology. Paleobiology 6:276–294.

HICKMAN, C. S. 1981a. Evolution and function of asymmetry in the archaeogastropod radula. Veliger 23:189–194.

HICKMAN, C. S. 1981b. Selective deposit feeding by the deep-sea archaeogastropod *Bathybembix aeola*. Mar. Ecol. Progr. Ser. 6:339–342.

HICKMAN, C. S. 1984. Implications of radular tooth-row functional integration for archaeogastropod systematics. Malacologia 25:143–160.

HICKMAN, C. S. & J. H. LIPPS. 1983. Foraminiferivory: selective ingestion of foraminifera and test alterations produced by the neogastropod *Olivella*. J. Foram. Res. 13:108–114.

HUBENDICK, B. 1957. The eating function in *Lymnaea stagnalis* (L.). Ark. Zool. 10:511–521.

KERTH, K. 1983. Radulaapparat und Radulabildung der Mollusken. I. Vergleichende Morphologie und Ultrastruktur.

Zool. Jb. Anat. 110:205–237; II. Zahnbildung, Abbau und Radulawachstum. Zool. Jb. Anat. 110:239–269.

LITTLER, M. M. & D. S. LITTLER. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. Amer. Natur. 116:25–44.

MÄRKEL, K. 1957. Bau und Funktion der pulmonaten Radula. Zeit. Wiss. Zool. 160:213–289.

MÄRKEL, K. 1966. Über funktionelle Radulatypen bei Gastropoden unter besonderer Berucksichtigung der Rhipidoglossa. Vie et Milieu, ser. A, 17:1121–1138.

McDONALD, G. & J. W. NYBAKKEN. 1978. Additional notes on the food of some California nudibranchs with a summary of known food habits of California species. Veliger 21:110–119.

MORRIS, T. E. 1980. Morphological and functional dynamics of the rhipidoglossan radula of *Tegula funebralis* (Mollusca: Gastropoda). Master's Thesis, Paleontology, Univ. Calif., Berkeley. 145 pp.

MORRIS, T. E. & C. S. HICKMAN. 1981. A method for artificially protruding gastropod radulae and a new model of radula function. Veliger 24:85–90.

NYBAKKEN, J. W. 1970. Correlation of radula tooth structure and food habits of three vermivorous species of *Conus*. Veliger 12:316–318.

NYBAKKEN, J. & G. McDONALD. 1981. Feeding mechanisms of west American nudibranchs feeding on Bryozoa, Cnidaria and Ascidiacea, with special respect to the radula. Malacologia 20:239–449.

RADWIN, G. E. & H. W. WELLS. 1968. Comparative radular morphology and feeding habits of muricid gastropods from the Gulf of Mexico. Bull. Mar. Sci. 18:72–85.

RUNHAM, N. W. & P. R. THORNTON. 1967. Mechanical wear of the gastropod radula: a scanning electron microscope study. J. Zool. (Lond.) 153:445–452.

STENECK, R. S. 1982. A limpet-coralline alga association: adaptations and defenses between a selective herbivore and its prey. Ecology 63:507–522.

STENECK, R. S. 1983. Escalating herbivory and resulting adaptive trends in calcareous algal crusts. Paleobiology 9:44–61.

STENECK, R. S. & L. WATLING. 1982. Feeding capabilities and limitation of herbivorous mollusks: a functional group approach. Mar. Biol. 68:299–319.

TAYLOR, P. D. 1981. Bryozoa of British Portland beds (Upper Jurassic). Paleontology 24:863–875.

VOIGT, E. 1977. On grazing traces produced by the radula of fossil and recent gastropods and chitons. Pp. 335–346. *In:* T. P. Crimes & J. C. Harper (eds.), Trace fossils 2. Geol. J. Spec. Issue 9.